

Relationships between woody vegetation and geomorphological patterns in three gravel-bed rivers with different intensities of anthropogenic disturbance

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Abstract

We compared three gravel-bed rivers in north-eastern Italy (Brenta, Piave, Tagliamento) having similar bioclimate, geology and fluvial morphology, but affected by different intensities of anthropogenic disturbance related particularly to hydropower dams, training works and instream gravel mining. Our aim was to test whether a corresponding difference in the interactions between vegetation and geomorphological patterns existed among the three rivers. In equally spaced and sized plots (n=710) we collected descriptors of geomorphic conditions, and presence-absence of woody species. In the less disturbed river (Tagliamento), spatial succession of woody communities from the floodplain to the channel followed a profile where higher elevation floodplains featured more developed tree communities, and lower elevation islands and bars were covered by pioneer communities. In the intermediate-disturbed river (Piave), islands and floodplains lay at similar elevation and both showed species indicators of mature developed communities. In the most disturbed river (Brenta), all these patterns were simplified, all geomorphic units lay at similar elevations, were not well characterized by species composition, and presented similar persistence age. This indicates that in human-disturbed rivers, channel and vegetation adjustments are closely

1 linked in the long term, and suggests that intermediate levels of anthropogenic disturbance, such as
2 those encountered in the Piave River, could counteract the natural, more dynamic conditions that
3 may periodically defragment vegetated landscapes in natural rivers.
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7 **Keywords:** fluvial morphology; gravel mining; riparian vegetation; hydropower dams; training
8 works; intermediate disturbance hypothesis.
9

1. Introduction

The interactions between biological drivers brought by plants and physical drivers mediated by water and sediment flows have received a lot of attention from scientists because of their complexity [8]. Fluvial dynamics influence the way riparian vegetation establishes and develops. In turn, riparian vegetation plays a crucial role in rivers, stabilizing the banks, deepening the main channel, and reducing the number of channels [64,65].

Unregulated large gravel-bed river systems may exhibit complex, dynamic and diverse multi-channel morphology [5]. The geomorphological processes creating the pattern of multiple channel belts and the morphology of the individual channel belts in these rivers are controlled, in many different ways, by climate and geology [11,19,68]. However, over periods of major human interference, many rivers have become dominated by incision and narrowing, resulting in relatively simpler channel forms [16, 18]. The recruitment of different tree species depends on the occurrence of bank erosion on floodplains and islands, formation of new, bare alluvial surfaces, and suitable hydrological conditions. Human pressures may therefore lead to either a reduction or expansion of vegetation in rivers [46], eventually producing non-natural equilibrium states [26] that may determine centuries of channel adjustment [6]. These patterns are common in large rivers of Europe [20]. For example, in the Iberian peninsula, Lobera et al. [33] showed that hydrological regulation reduces the magnitude and frequency of floods, decreases downstream sediment supply, resulting in the loss of active bars as they become colonized by vegetation and are not subject to sediment remobilization, except during very large floods. In highly regulated rivers of the Alps, the dynamic maintenance of pioneer vegetation on gravel bars and young islands is hampered by the reduction in frequency of relevant flood magnitudes [29,40]. Accordingly, in the north-eastern Italian pre-Alps, Picco et al. [49] identified a missing correspondence between woody communities transversal succession and geomorphological gradients in a gravel-bed river affected by gravel mining and hydropower plants.

Although the effect of hydrological regulation on fluvial geomorphological configuration and its interaction with riparian vegetation has already been demonstrated [37], to our knowledge quantitative data are still missing on these interactions in rivers subject to different levels of disturbance, but comparable in terms of climate, geology, and biogeography.

There are many possible anthropogenic drivers of disturbance and each of them may have effects on the relationship between vegetation and geomorphology at specific spatial and temporal scales [57]. The present work applied a sampling design consisting of a set of cross-section transects established in several sub-reaches distributed along three large gravel-bed rivers located in the south-eastern pre-Alps. At this scale, the three studied rivers can be differentiated in terms of level of intensity of

a set of stressors that included dam density, flow regulation and river fragmentation [67]. Landscape indicators of such stressors were the presence of instream gravel mining sites, hydroelectric power plants, channel embankments and floodplain croplands [14,30], as further explained in the study area description.

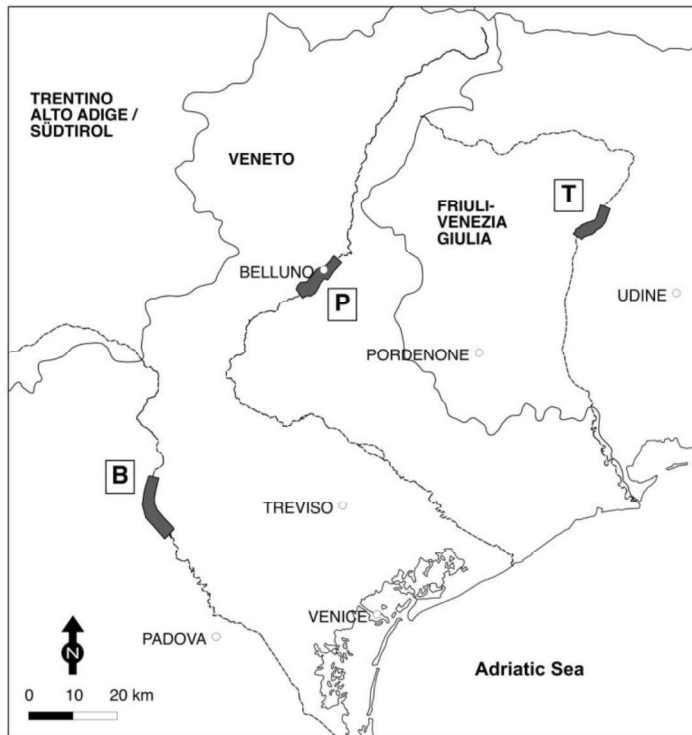
In equally spaced and sized plots we collected quantitative, semi-quantitative, and qualitative descriptors of geomorphic conditions, coupled with presence-absence of tree and shrub species. Given the uniformity of biogeographic conditions and position along the river continuum, we compare the relationships between geomorphic and sedimentary structures and woody vegetation characteristics. This makes it possible to test the validity of the intermediate disturbance hypothesis, by studying how the relationships between vegetation and geomorphological pattern change along a gradient of intensity increase in anthropogenic disturbance. The intermediate disturbance hypothesis, earlier developed by Grime [17], argues that higher numbers of species coexist at intermediate levels of disturbance. In this condition, more lively competitive interactions avoid the prevalence of few specialized species [54]. This hypothesis has been tested in several environments, including rivers [69] and extended to more complex expressions of diversity than simply species richness [39]. Here, our hypothesis is that the complexity of the relationship between vegetation and geomorphological pattern in the most disturbed river is simplified due to the adjustment of its morphological pattern to the human induced low variability of water and coarse sediment transport [7,60]. In addition, we might also expect that the complexity shown by the intermediate-disturbed river would be even higher than the less disturbed river.

2. Material and methods

2.1 Study area

The research has been conducted along three gravel-bed rivers (Brenta, Piave, and Tagliamento) located in north-eastern Italy (Fig. 1). They all fall within the Illyrian-Gardesan Dolomitic floral sector of the south-eastern pre-Alps [43], so have similar characteristics in terms of bioclimatic and geological features.

Figure 1



The surveyed sites are located where the rivers exit the main Alpine range and enter the Veneto plain, and have a similar morphological pattern, which is predominantly wandering-braided. However, they differ substantially in terms of anthropogenic disturbances over the basin and along the main channel, and this has had consequences on their current active channel width.

Table 1

	Drainage basin area (km ²)	Sediment yield (m ³ km ⁻² year ⁻¹)	Periods of intense gravel mining	Extraction yield (official data) (m ³ year ⁻¹)	Time of dam closure	Drainage area upstream from dams (%)	Bed incision occurred in the 20 th century * (m)
Brenta	1,567	250-275	1950s - 1980s	360,000 (from 1953 to 1977)	1954	40	2.5 - 5
Piave	3,899	180-200	1960s - 1980s	not available	1930s - 1950s	54	1-2
Tagliamento	2,580	400	1970s - early 1990s	1,100,000 (from 1970 to 1991)	1950s	3	0.5 - 1

*data refer to the reaches investigated here.

2.1.1 Brenta River

The Brenta river basin extends for 1,567 km² and the main channel is 174 km long. Since the 1950s, intense human pressures have affected the river, changing its morphological and vegetation dynamics. Indeed, a combination of gravel mining, construction of dams and check-dams in the upper basin, and of levees and groins in the middle course strongly affected the river morphology [62]. Gravel mining is considered as the most impacting human pressure [61], and it was carried out mainly between the 1950s and 1980s, mostly in the middle and lower course of river. The construction of 8 dams (storage capacity of about 64,500,000 m³) is considered as the second most important human alteration of river morphology, decreasing both flow and sediment discharges, disconnecting around 40% (Tab. 1) of the basin area from the lower river channel in terms of bedload transport [37]. Finally, along about 90% of the main course river training works (i.e. embankments reinforced with ripraps and groins) were built extensively and definitely decreased the lateral channel mobility. As a result of these pressures, the average channel width of the Brenta River narrowed from 442 m at the beginning of the 1800s, to 182 m in 1990, channel incision reached up to 5-8 m (mostly ranging from 2.5 to 5 m, see Table 1) during the most intense gravel mining period [61], and islands almost disappeared (Fig. 2a) [27,28,35,36,38,61]. Thanks to the imposition of regulatory constraints on commercial gravel extraction in the late 1990s, there has been a partial width recovery [37], which is anyhow quite limited because sediment supply to the river is greatly reduced by the presence of dams and torrent control works in the basin, and by bank protection limiting sediment input from lateral mobility.

Within a 15 km reach located between the villages of Nove and Fontaniva (drainage area 1,160 km², Fig. 2), three sub-reaches were identified for the analysis in the Brenta River. Field surveys were conducted along these three sub-reaches called Nove, Friola and Fontaniva, from upstream to downstream respectively (Fig. 2a). The Nove sub-reach presents a single straight channel, an average width of about 175 m, mean slope of 0.0039 m m⁻¹, and D₅₀ = 0.037 m. The Friola sub-reach has a wandering channel, mean width of about 280 m, mean slope of 0.0025 m m⁻¹, and D₅₀ = 0.035 m. Lastly, the Fontaniva sub-reach shows a braided morphology with average width of 375 m, mean slope of about 0.0030 m m⁻¹, and D₅₀ = 0.031 [52]. Island mean width is 10.1 m.

Following Surian and Rinaldi [60] conceptual models, this river adjusted to the human disturbances of the second half the 20th century mainly through channel narrowing, from braided to wandering morphology, combined with a significant incision (case H, Fig. 6 in [60]).

2.1.2 Piave River

The Piave river basin extends for 3,899 km² and the river channel flows for ~222 km between the Brenta and the Tagliamento rivers, reaching the Adriatic Sea a few kilometres north of Venice.

Hydropower dams, water abstractions for irrigation, sediment mining and torrent control works, as well as deforestation and reforestation phases influenced the river morphology [33,36]. Notably, during the 1930s–1950s dams were built along its channel network, leading to about 54% (Tab. 1) of the basin area disconnected from the lower river channel in terms of bedload transport, and between the 1960s and 1980s, there was intense sediment mining along the main channel [49]. As a result, the Piave River underwent narrowing and incision (see Table 1), and a progressive change from braided to a wandering/single-thread morphology, with the encroachment of riparian vegetation on the former active channel [7,44,47,55,59]. Widespread channel narrowing occurred in the range of 60-70% in the reach studied in this work [7]. As for the Brenta River, the ban on commercial gravel mining in the 1990s likely resulted in a ceasing of bed degradation and permitted a limited channel expansion during flood events in the first decade of the 2000s.

Field surveys were conducted along two sub-reaches called Belluno and Praloràn, from upstream to downstream (Fig. 2b). The drainage area of the basin at Belluno is 1,964 km². The Belluno sub-reach has a predominantly braided morphology, mean width of about 375 m, mean slope of 0.0033 m m⁻¹, and D₅₀ = 0.045 m. The Praloràn sub-reach has a wandering pattern with a mean active channel width ~250 m, mean slope of 0.0048 m m⁻¹, and D₅₀ = 0.040 m [52]. Island mean width is 24.80 m.

This river responded to the above-mentioned anthropogenic pressures of the second half of the 20th century mainly through channel narrowing, with a widespread shift from braided to wandering morphology and a moderate incision (case F, Fig. 6 in [60]).

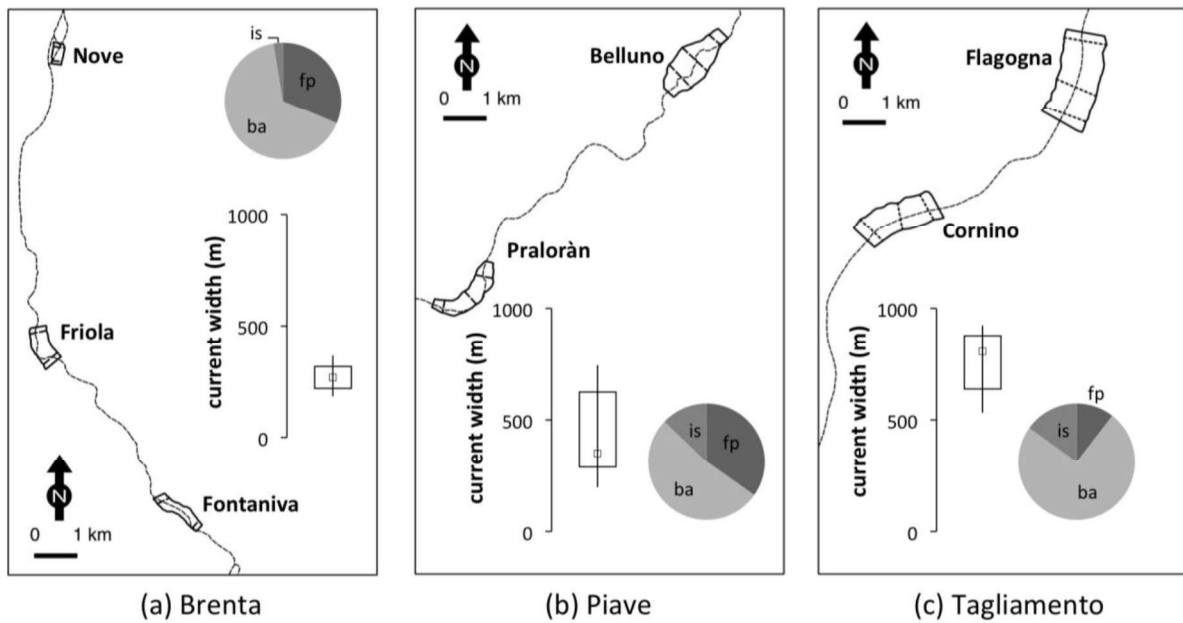
2.1.3 Tagliamento River

The Tagliamento river basin covers around 2,580 km² and the river flows for about 178 km to the Adriatic Sea, representing an important ecological corridor connecting the Alpine and Mediterranean zones. The Tagliamento River can be considered as 'the most intact and natural river in the Alps' [32,40,53,69], as well as 'a reference ecosystem for the Alps but also as a model ecosystem for large temperate rivers' [66]. Human pressures in the basin relative to water and sediment management are minor, in fact just about 3% of the basin area is disconnected from the lower river channel in terms of bedload transport (Tab. 1) and there are torrent control works (check dams) only in some of the tributaries. The current morphological processes can be considered to take place under near natural conditions, with relatively frequent flows able to erode woody vegetation [63]. However, sediment mining was quite extensive in the river in the 1970s-1990s period (Tab. 1), and this led to a moderate channel incision (up to 3 m in some reaches, [62]) In the surveyed sub-reaches only small channel width variations have been recorded in the period 1954-2009 [70].

Field surveys were conducted in two sub-reaches named Cornino and Flagogna, from upstream to downstream (Fig. 2c). The Cornino sub-reach presents a bar-braided setting, a mean width of about 800 m (ranging from a maximum of 1000 m to a minimum of 700 m), mean slope of 0.0030 m m^{-1} , and $D_{50} = 0.035 \text{ m}$. The Flagogna sub-reach features a wandering setting with active channel width of around 600 m (between 300 and 800 m), mean slope of 0.0030 m m^{-1} , and $D_{50} = 0.035 \text{ m}$ [4,52]. Island mean width is 23.80 m.

In the last century, also the Tagliamento River was affected by channel narrowing in response to gravel mining, but in this case the morphological pattern remained braided, and the incision was estimated to be quite limited (0.5–1.0 m, [63] and [70]). Now that commercial gravel mining is banned, the current hydro-morphological processes in this river are much less altered than the Piave and Brenta, as already mentioned above (case C, Fig. 6 in [60]).

Figure 2



2.2 Materials and methods

2.2.1 Data collection

Field surveys were conducted in three sub-reaches along the Brenta River and two sub-reaches per river along the Piave and Tagliamento, all of them featuring either wandering or braided morphology. Six cross-section transects were sampled in each river (Tab. 2) and topographically surveyed in 2010, using a Differential Global Positioning System (dGPS) (average accuracy $\pm 0.025 \text{ m}$). The surveyed length of the cross sections was determined by the lateral extent of the floodplain as defined by topographic, soil and hydrological characteristics. Along each cross

section, 4x4 m plots spaced 10 m apart were identified along the cross-section transects. The plots were positioned by dGPS and identified in the field using tapes and a compass in order to establish a square plot area. A total of 710 plots were positioned, of which 83 were not surveyed because they lay on low-flow channels with flowing water. The number of surveyed plots per cross section ranged from 14 to 66 (Tab. 2).

Table 2

River	Sub-reach	Cross-section transect ⁽¹⁾	Number of plots ⁽²⁾	Total length (m) ⁽³⁾
Brenta	Nove	1	17	256
		2	13	214
	Friola	1	26	396
		2	23	424
	Fontaniva	1	15	228
		2	21	312
Piave	Belluno	1	19	368
		2	53	760
		3	51	760
	Praloràn	1	25	410
		2	25	382
		3	14	256
Tagliamento	Cornino	1	66	1,012
		2	62	998
		3	63	998
	Flagogna	1	38	606
		2	43	648
		3	53	732

(1) From upstream to downstream (2) low-flow channel excluded (3) whole length, including low-flow channels

All woody species found on plot areas were identified and diameter at breast height (DBH) of all individuals with DBH > 3 cm was measured. Tree age class was measured by coring with a Pressler borer the largest individual with DBH > 10 cm (1: no trees with DBH > 10 cm, 2: < 5 y, 3: 6-15 y, 4: 16-25 y, 5: > 25 y). The number of rings was checked in the laboratory using the professional system CATRAS (Computer Aided Tree-Ring Analysis System) [1]. On each plot with a developed soil, fine sediment depth was determined by digging a small trench down to the gravel layer. On plots with coarse sediments (gravel), the surface grain size distribution was calculated by measuring the b-axes of 30 coarse (gravel and cobbles) elements.

The discrete landform types (floodplains, bars, islands) relative to each plot were classified in the field based on a combination of characteristics such as elevation above thalweg, substrate grain size and vegetation cover. Main and secondary channels were identified as low-relief areas of the cross sections featuring an obvious preferential flow path. Bars were identified as higher-relief gravel units exposed at lower flows, either bare or supporting only annual vegetation and a small accumulation of river-transported plants and large wood. Islands were identified as vegetated patches completely surrounded by either channels or exposed gravel [68,42]. In all three rivers, the 20th century incision phase turned the pre-incision floodplains, normally inundated every 1-3 years [24,25], into low terraces that are not reached by the same recurrence interval floods. However, similarly to what was done in Picco et al. [49], the recent, low terraces were considered floodplains in this study, as other, more frequently inundated vegetated landforms at channel margins – post-incision floodplains – are still missing in the studied rivers.

In order to establish the persistence of each landform type, a multi-temporal analysis was performed using aerial photos of the same areas dating to 1981, 1990, 1994, 1999, 2006 and 2010 for the Brenta River, to 1960, 1970, 1980, 1991, 1999, 2006, and 2010 for the Piave River, and to 1954, 1970, 1986, 1996, 2005 and 2010 for the Tagliamento River. The geomorphic persistence is the age of the oldest photograph in which no changes of the current landform type attribution are detectable. A synthesis of the surveyed variables is reported in Table 3.

Table 3

Group	Variable	Math type ⁽¹⁾	Code	Definition
Geomorphology	Landform type	b		fb: floodplain; ba: bar; is: island
	Elevation	c	E	Elevation above thalweg
	Grain size	c	G	Surface mean grain size of 30 randomly selected elements
	Fine sediment	b	S	Fine sediment occurrence (transformed from fine sediment depth)
	Geomorphic persistence	c	M	Persistence of each landform type
Stand	Tree age	d	T	Mean age of the largest tree (DBH>10cm) 1: no trees with DBH > 10 cm; 2: < 5 y; 3: 6-15 y; 4: 16-25 y; 5: > 25 y
	Tree diameter	c	D	Mean diameter at breast height (DBH) of individuals with DBH > 3 cm

⁽¹⁾ The mathematical types are classified as o (ordinal), b (binary), d (quantitative discontinuous), and c (quantitative continuous)

2.2.2 Fluvial landforms analysis

To enable comparisons among types of landforms and rivers we tested differences between their means. Because plots were nested within sub-reaches, the use of a random effects model was necessary to take into account the correlation within plots belonging to the same sub-reach, by assigning a random effect for each plot within each sub-reach. We applied linear mixed models (LMM), after transformation of the original values, where needed, according to each river data distribution. In some cases, violations of assumptions led to using the Akaike information criterion to select a specific variance structure [71]. Fine sediment depth was transformed in the presence / absence of sediment because of its wide variability within landform types and a generalized linear mixed-effects model (GLMM) was applied. Multiple comparisons were tested using Tukey all-pair comparisons between the landform types.

2.2.3 Assessment of association between landform types and woody species

To assess the strength of the association between single woody species and landform types within rivers, we conducted an indicator species analysis with $\alpha = 0.05$ [9]. Good indicator species are those that are both abundant in one or more specific types (specificity) and predominantly found in these types (fidelity). As a measure of association, we used Pearson's phi coefficient of association corrected for unequal group sizes [10]. The statistical significance of each relationship was verified by a permutation test described in Dufrêne and Legendre [13] with 999 permutations.

2.2.4 Analysis of the relationships between species composition, stand and geomorphic conditions

Redundancy analysis (RDA) was used to describe and visualize the relationships between species composition, stand conditions and geomorphic properties, across the groups of rivers and landform types. We followed two approaches. First, the rivers were analysed together, using stand and geomorphic variables as quantitative constraints and combinations of river and landform types as factors. For this analysis we produced ordination plots, limited to those plant species with a goodness of fit $> 15\%$. With this constrained ordination approach we attempted to explain differences in species composition by differences in landform types, stand conditions and geomorphic properties. We then conducted three RDA analysis for each river separately, where we used only geomorphic quantitative variables and landform types as factors. The aim was to assess the amount of constrained species variance, i.e. the variance of the species matrix explained by geomorphological patterns. In both cases, the variables were standardized prior to RDA and a permutation test was used to assess the significance.

All analyses were performed by the software R [51] using the function 'lme' of the package 'nlme' 3.1-115 for LMM [50], function 'glmer' of the package 'lme4' 1.1-5 for GLMM [3], function 'glht' of

the package 'multcomp' 1.3-2 [23] for Tukey all-pair comparisons and the function 'rda' of the package 'vegan' 2.0-10 [41] for RDA.

3 Results

3.1 Fluvial landforms characterization

Amongst the 627 plots that were on floodplains (n=135), bars (n=416) or islands (n=76), 234 contained at least one woody species. The rest of the plots were located in low-flow channels and were not further surveyed or analysed. Different frequencies of landform types were identified in the surveyed sub-reaches (Fig. 2). Mixed models were used to test for differences in geomorphological variables and stand conditions between landform types. Given the very low numbers of islands in the Brenta River, the differences in this river were tested only between floodplains and bars.

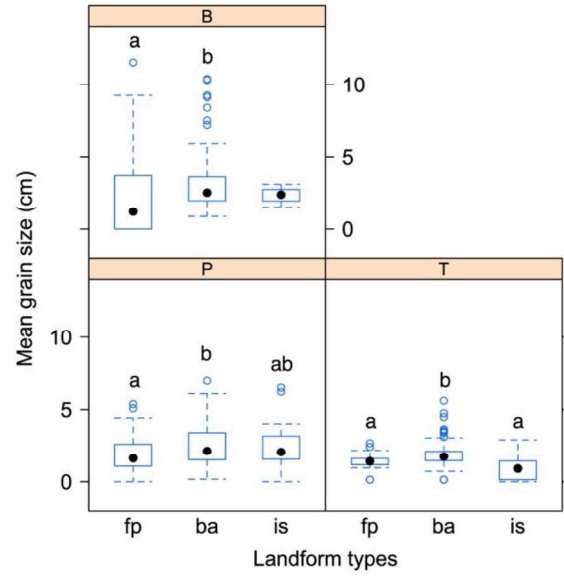
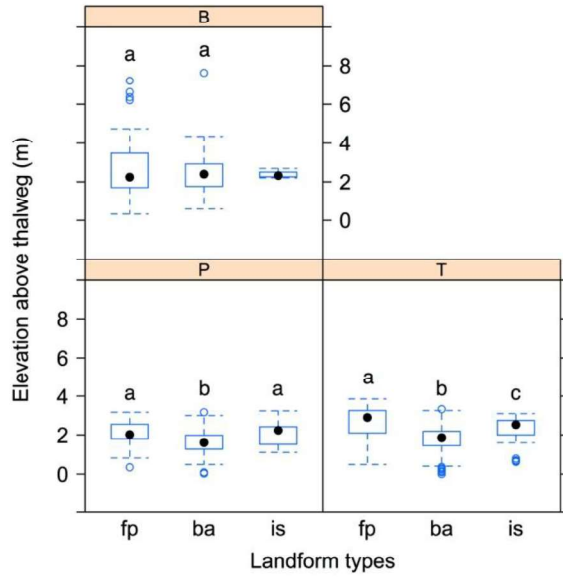
The Brenta River did not show any significant difference in elevation (Fig. 3a) and geomorphic persistence (Fig. 3d) between floodplains and bars. However, its floodplains had lower grain size ($P < 0.001$, Fig. 3b) and more fine sediments ($P < 0.001$, Fig. 3c) than bars. Age and mean DBH of trees were significantly higher on floodplains than on bars (Fig. 4).

In the Piave River, floodplain and island plots resulted as being significantly higher than bars ($P < 0.001$, Tukey contrasts, Fig. 3a), while islands and floodplains lay at same elevations ($P = 0.849$, Tukey contrasts, Fig. 3a). Bars featured fewer fine sediments ($P < 0.001$, Tukey contrasts, Fig. 3c). Floodplains had significantly lower mean grain size than bars, but this was not the case for the islands, whose differences with respect to both other landform types were not statistically different (Fig. 3b). As expected, floodplains featured a longer persistence than bars ($P < 0.001$, Tukey contrasts, Fig. 3d). The wide variability of persistency ages recorded on islands (Fig. 3d) is the reason for the absence of any difference between them and both bars and floodplains. Tree age and mean diameter were higher on floodplains and islands than on bars ($P < 0.001$, Tukey contrasts, Fig. 4).

In the Tagliamento River, elevation followed a marked trend: floodplains > islands > bars ($P < 0.001$ and $P < 0.05$ for Tukey contrasts with bars, and between floodplains and islands, respectively, Fig. 3a), with absolute differences in mean between the latter of 38 cm. Mean grain size was smaller on bars ($P < 0.05$, Tukey contrasts, Fig. 3b), but was remarkably similar on floodplains and islands ($P = 0.99$, Tukey contrasts, Fig. 3b).

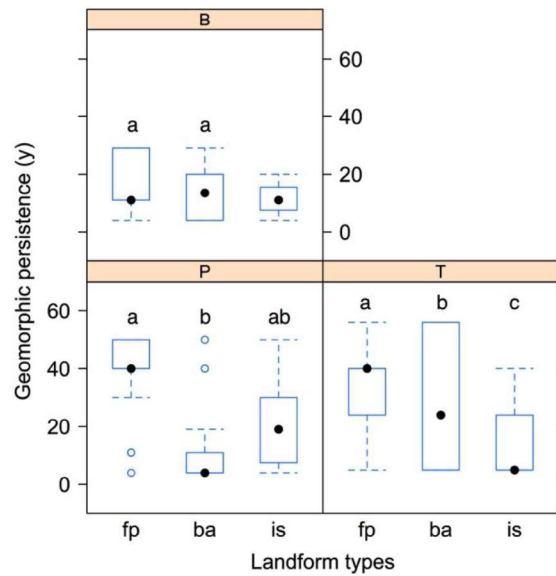
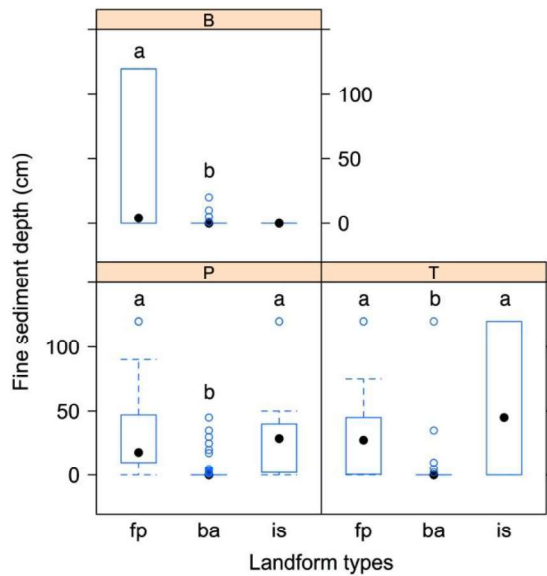
Figure 3

a) b)



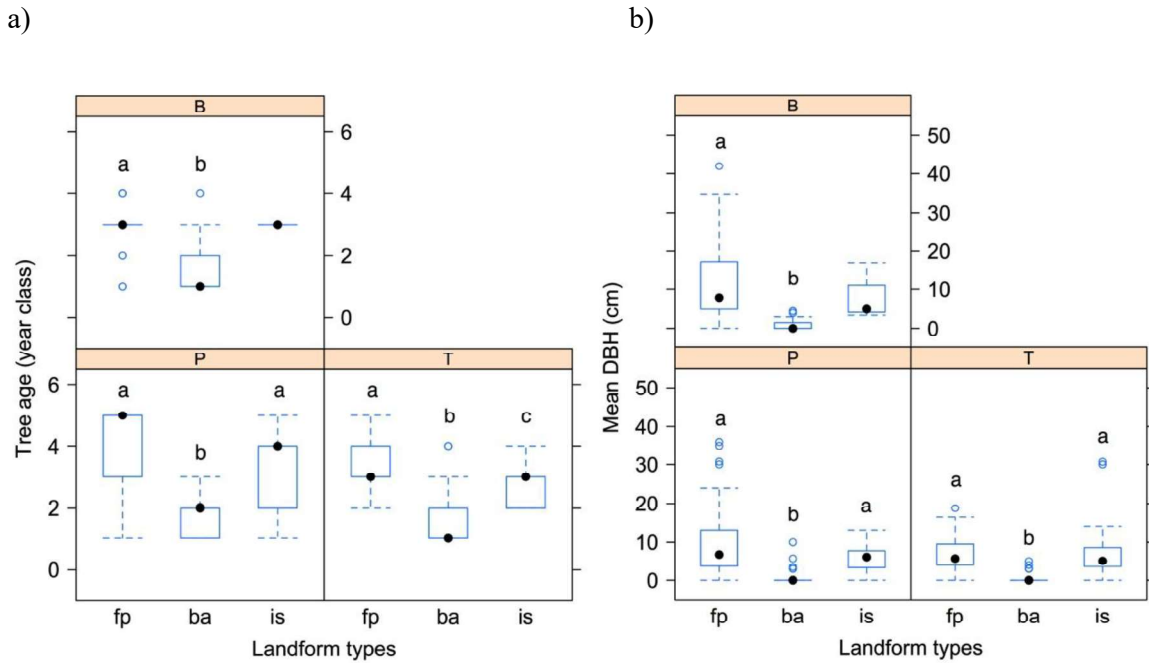
c)

d)



The same pattern is clear comparing values of fine sediment (Fig. 3c). In contrast, floodplains were of longer persistence if compared with either bars ($P < 0.001$, Tukey contrasts, Fig. 3d) or islands ($P < 0.001$, Fig. 3d). The latter were also less persistent than bars ($P < 0.05$, Tukey contrasts, Fig. 3d). The same trend observed for elevation was observed for tree age, with floodplains $>$ islands $>$ bars (Fig. 4a). Finally, the high presence of relatively large outlier trees on bars generated a non-structured heterogeneity in the data, which must be interpreted as a signal of a casual distribution of large trees among landform types (Fig. 4b).

Figure 4



3.2 Association between landform types and woody species

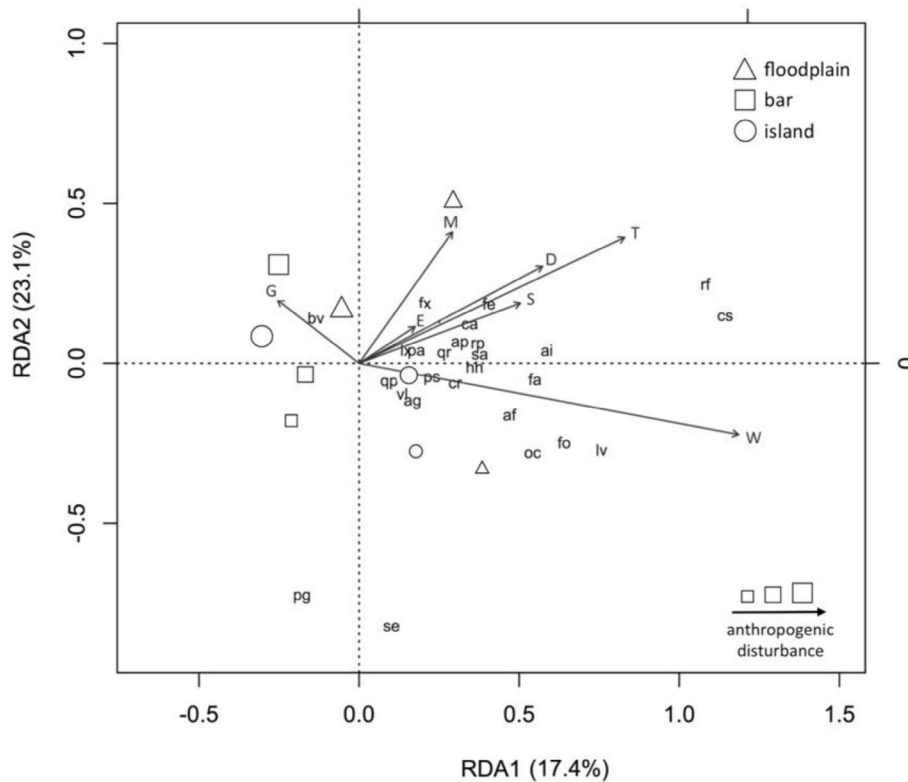
From the total number of 60 woody species, 28 showed a statistical significance of association with landform types within rivers ($P < 0.05$). As shown in Table 4, the Tagliamento is the river with the highest number of indicator species ($n=40$), followed by the Piave ($n=31$), and Brenta ($n=13$). As expected from its definition, the landform type with the richest matching patterns is the floodplain, while, in general, the Brenta River was remarkably poorly characterized. Floodplains along the Tagliamento River had the highest number of indicator species not shared with other types of landforms (e.g., *Alnus glutinosa* and *Quercus pubescens*), but also a higher number of species shared with other types than the Piave River. In contrast, islands and floodplains of the Piave River showed the same number of indicator species. Islands of the Piave River featured two drought tolerant species (*Fraxinus ornus*, *Ostrya carpinifolia*), which were not associated to its floodplains, but were associated to the more heterogeneous Tagliamento floodplain. It is noteworthy that *Quercus robur* was associated only to the islands of the Piave River.

Table 4

Brenta			Piave			Tagliamento			Species	IndVal	p-value
fp	ba	is	fp	ba	is	fp	ba	is			
■									<i>Vitis vinifera</i>	0.239	0.045
		■							<i>Berberis vulgaris</i>	0.781	0.001
			■						<i>Fraxinus angustifolia</i>	0.442	0.005
			■						<i>Sambucus racemosa</i>	0.254	0.045
					■				<i>Quercus robur</i>	0.482	0.008
						■			<i>Alnus glutinosa</i>	0.482	0.003
						■			<i>Crataegus monogyna</i>	0.452	0.009
						■			<i>Quercus pubescens</i>	0.343	0.034
						■			<i>Pyrus pyraister</i>	0.297	0.024
			■			■			<i>Acer pseudoplatanus</i>	0.409	0.002
						■		■	<i>Ligustrum vulgare</i>	0.559	0.004
			■		■	■			<i>Frangula alnus</i>	0.471	0.033
			■		■	■			<i>Fraxinus excelsior</i>	0.466	0.01
			■		■	■			<i>Robinia pseudoacacia</i>	0.443	0.023
			■		■	■			<i>Corylus avellana</i>	0.42	0.021
			■			■		■	<i>Alnus incana</i>	0.592	0.006
			■			■		■	<i>Amorpha fruticosa</i>	0.483	0.05
					■	■		■	<i>Fraxinus ornus</i>	0.559	0.001
					■	■		■	<i>Ostrya carpinifolia</i>	0.517	0.002
	■	■				■	■	■	<i>Salix purpurea</i>	0.43	0.042
■			■			■		■	<i>Hedera helix</i>	0.368	0.045
				■	■		■	■	<i>Salix daphnoides</i>	0.352	0.035
			■		■	■		■	<i>Clematis vitalba</i>	0.414	0.03
■			■		■	■		■	<i>Rubus caesius</i>	0.793	0.001
■			■		■	■		■	<i>Cornus sanguinea</i>	0.735	0.001
■			■		■	■		■	<i>Salix alba</i>	0.46	0.04
■	■	■		■	■	■	■	■	<i>Salix eleagnos</i>	0.854	0.001
■	■	■		■	■	■	■	■	<i>Populus nigra</i>	0.81	0.001

3.3 Relationships between woody species composition, geomorphology and stand conditions

Figure 5



RDA results showed that the proportion of variance explained by all environmental factors was 30.0% ($R^2_{adj}=0.27$). The significance test for all constraints simultaneously with 999 permutations yielded a value of $P < 0.001$ ($F_{15,377} = 10.8$), hence it is not very likely that the observed pattern was just random. Single constraints were also all significant ($P < 0.05$). We can thus be confident that we described an actual pattern of correlation between vegetation, geomorphic and stand conditions.

The graph in Fig. 5 reports the differences among species composition that can be related to differences in landform types and environmental variables. The landform types, geomorphic and stand variables (biplot scores) and the species loadings on the first two axes (RDA1: 17.4% explained variance, RDA2: 23.1% expl. var.) are shown. The species scores should be interpreted as vectors indicating the direction of larger abundance for the species. The direction from the origin to the biplot score for constraining variables shows sites with higher values for the environmental variable. The centroid scores show the average position that is predicted for sites of the same landform type.

The graph shows that number of woody species (W), fine sediment (S), tree age (T) and diameter (D), and grain size (G) played an important role in the dispersion of the sites along the first axis. The second axis follows a gradient of increase in geomorphic persistence (M). On the upper right side of the graph, a group of species found mainly on relatively mature soils, with presence of fine sediment (S) and longer geomorphic persistency (M), which develop in mature stands with higher

mean DBH (D) and tree ages (T), contrast with one indicator species on the upper left, *Berberis vulgaris* (bv), which is found on coarser soils (G).

Elevation above thalweg (E) is correlated to D, T and S, but does not describe steep gradients. On the contrary, a sharp increasing trend of woody species numbers (W), in the opposite direction to mean grain size increase (G), may be observed with the presence of drought tolerant species, like *Fraxinus ornus* (fo), *Ligustrum vulgare* (lv), and *Ostrya carpinifolia* (oc).

Salix eleagnos (se) and *Populus nigra* (pg) seem to be more abundant on the Tagliamento islands and floodplains, indicating similar pioneer site conditions on these two landform types. All landform types of the Brenta River are remarkably poorly differentiated and have a distinct increase in mean grain size gradient, with no particular indicator species. This is also true for bars of the other three rivers, but the Brenta is the only river in which this could also be extended to islands and floodplains, which show a very similar pattern to the bars.

The composition of the Piave river floodplain is the more strongly dependent on geomorphic patterns amongst the landform types, showing a notably higher geomorphic persistence, which allows the development of mature stage tree species, like *Fraxinus angustifolia* (fx) and *F. excelsior* (fe). The islands of the Piave River feature tree species with different ecological amplitudes, like *Quercus pubescens* (qp), *Viburnum lantana* (vl), *Alnus glutinosa* (ag), *Pinus sylvestris* (ps) and *Crataegus monogyna* (cr). In contrast, floodplains and islands of the Tagliamento River have a rich pool of species with uniform drought tolerance, as mentioned above.

The three RDA analysis conducted on the rivers separately were all significant ($P < 0.001$ with 999 permutations) and showed that the species variance explained by geomorphological patterns was higher in the Piave ($\sigma^2 = 0.75$), followed by the Tagliamento ($\sigma^2 = 0.66$) and Brenta River ($\sigma^2 = 0.41$).

4. Discussion

Prior work has documented the influence and impact of anthropogenic disturbance on the development of vegetation on bars, banks, and floodplains, and hence on channel morphology. Hupp and Osterkamp [24], underlined that the distribution pattern of riparian vegetation is strongly related to the hydrological and geomorphic conditions which, in turn, are affected by a wide array of human pressures [25,30]. For instance, channel adjustment following human control may lead to the loss of association between riparian tree communities and the corresponding geomorphological gradients. For example, Dufour et al. [12] have documented the transition from a braided to wandering pattern after years of human activity, coupled with riparian woodland expansion and landscape diversity increase in the riparian zone. Picco et al. [49] have recently shown that mean grain size may not differ between either landform or vegetation types in a regulated river. However,

these studies have focused on just one regulated river which hinders an immediate comparison between different levels of anthropogenic disturbance.

In this study we applied the same sampling design to three multi-channel gravel-bed rivers, located in the same biogeographical region and having the same geological substrate, hence with the same potential vegetation. The three rivers reflect a gradient of anthropogenic disturbance. In the Tagliamento River, human induced impacts are reduced, large tributaries flow with a natural regime and no dams have been built along the mainstream. In the Piave River, instream gravel mining, hydroelectric plants and embankments have changed the river channel to an intermediate degree. Lastly, in the Brenta River, hydroelectric plants, irrigation purposes, dams and intense instream gravel mining have intensely changed the natural settings of the river. This makes it possible to test the validity of the intermediate disturbance hypothesis by studying how the relationship between vegetation and geomorphological pattern changes along a gradient of increase of a complex of anthropogenic river disturbance factors.

We found that in the most natural Tagliamento River, spatial succession of woody communities from the floodplain to the channel conforms to a profile where developed tree communities belong to floodplains, while lower-elevation and more disturbed islands and bars are covered by pioneer communities. Island vegetation is subject to high turnover caused by occasional massive erosion and quick regrowth of willows and poplars, which are the main shrub and tree species [29]. Species of mature stages (e.g., *Fraxinus excelsior*) are confined to floodplains. However, they share drought tolerant indicator species with islands. In the intermediate-disturbed Piave River, islands and floodplains lie at similar elevation and both show species indicators of mature developed community stage, like *Quercus robur*. In the most disturbed Brenta River, all these patterns are disrupted, and all landform types lie at similar elevations and their species composition is not well characterized. The geomorphic persistency is much longer in the floodplains of the intermediate-disturbed river than in the less-disturbed river. In the most disturbed river, finally, it is noteworthy that the persistence time is similar among the different landform types.

These findings extend those of Gilvear et al. [15], confirming that elevation above thalweg and grain size are the most important variables controlling the moisture of in-channel vegetated patches, and hence morphological and sediment diversities are important factors supporting plant species richness and habitat diversity in non-regulated rivers. Moreover, they confirm that in the active zone of a natural island-braided Alpine river, succession will never reach the stage of more mature softwood forest or hardwood forest that are typical of higher elevations and less frequently disturbed sites on floodplains [29], but this could happen in intermediate-disturbed rivers. In addition, we noted that grain size is an indicator of heavy human impact and simplification of

1 riparian vegetation composition, which levels out any distinction between floodplains, islands, and
2 even bars.

3 Previous work by Comiti et al. [7] concluded that planform channel adjustment in the Piave River,
4 i.e. the intermediate-disturbed river, is due to alteration of sediment supply rather than flow regime,
5 and is not necessarily linked to major bed incision or aggradation. In contrast with what has been
6 observed in the most natural river, even a slight bed incision from gravel mining implies
7 encroachment of vegetation and channel narrowing, and only infrequent flood events may erode the
8 islands.
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10 The islands present in the intermediate disturbed river are generated by a process of vegetation
11 growth and surface aggradation (building islands) rather than from floodplain dissection, and no
12 woody communities clearly dominate, as previously demonstrated by Picco et al. [49]. However,
13 this is not the case in the Brenta River where limitation of sediment supply by dams is higher than
14 in the Piave. For the Tagliamento River, Surian et al. [63] argue that an expansion of in-channel
15 vegetated areas (i.e. islands) can be envisaged for the next years because of a marked increase in the
16 availability of wood from the channel margins, which are now much more forested than in previous
17 decades.
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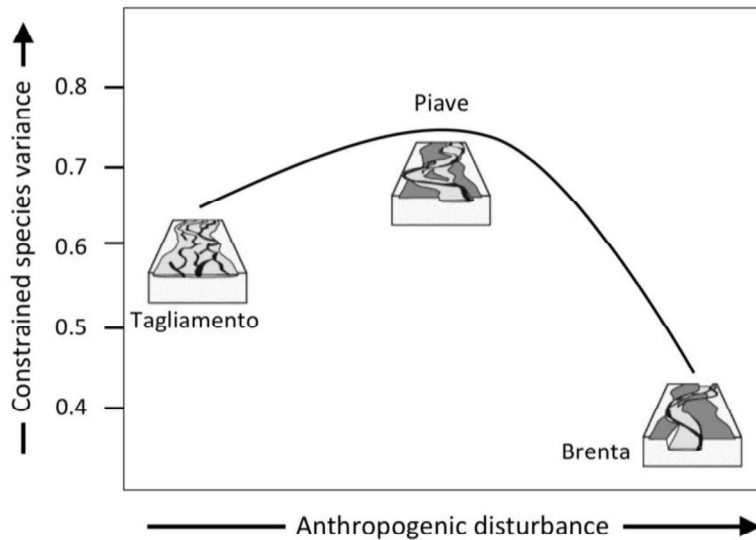
19 This study therefore indicates that different levels of human impacts may lead to the transformation
20 of natural geomorphic-vegetation relationships. In part, this conforms to the idea that island
21 development in natural braided rivers seems to be a form of cyclical succession that does not
22 correspond to the standard succession and zonation within Alpine floodplains [29]. Apparently, this
23 is also valid for non-regulated rivers.
24

25 Most notably, this is the first study to our knowledge to provide evidence of the higher geomorphic
26 persistence that may be reached by floodplains in intermediate-disturbed rivers, which could host a
27 woody flora of higher mature stages than more natural rivers. This provides compelling evidence
28 for long-term integration of channel and corresponding riparian vegetation adjustment in regulated
29 rivers.
30

31 Our results suggest that intermediate levels of disturbance reduce the natural fluvial dynamics that
32 periodically fragment vegetated landscapes in natural rivers. This clearly supports the intermediate
33 disturbance hypothesis [17]. Here we expressed diversity not in terms of species richness, but in
34 terms of variance of the species matrix explained by geomorphological patterns. We have shown
35 that the influence of the geomorphological variability on species variance is stronger where
36 anthropogenic disturbance is intermediate (Piave River), and reduces both where human disturbance
37 is lower (Tagliamento River) and higher (Brenta River). We suggest that the relationships between
38 species variance constrained by geomorphological patterns and anthropogenic disturbance in the
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three rivers can be schematized according to the intermediate disturbance hypothesis, as in Figure 6. The pattern differs from the idealized hypothetical curves (see for example [69]), as expected for a real natural system, but confirm the general predictions of the intermediate disturbance hypothesis.

Figure 6



5. Conclusions

We have demonstrated that different levels of anthropogenic disturbance in three gravel-bed rivers can be discriminated by morphological and stand variability among floodplains, bars and islands. We have also shown that woody species distribution patterns interact more sharply with certain morphological variables related to the alteration of natural fluvial processes, namely mean grain size and geomorphic persistence. We found that the intermediate-disturbed river features higher geomorphic persistence of its floodplain if compared with the other two rivers and this has a strong influence on riparian vegetation patterns. The permanence of some species that are indicators of mature stands is apparently related to the observed interactions between morphological and vegetation patterns as mediated by human impacts. Moreover, islands, which are landform types commonly covered mostly by pioneer riparian communities with only a few older patches, may display, in intermediate disturbance regimes, an unusually high heterogeneity of ecological amplitudes of their associated species.

Plant communities along the intermediate-disturbed river are characterized by important relict alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (communities related to *Salicetum albae* and *Alnetum incanae*), riparian mixed forests related to the *Alno-Ulmion*, and associated

1 wetlands, which host critically endangered plant species at provincial level, like *Potamogeton*
2 *coloratus* [2, 31], and animal species, e.g. insects and breeding birds associated with particular
3 microhabitats in mature forests, such as rot holes in old senescent trees, sap runs, water-logged
4 cavities and dead wood [21]. The composition of these communities might indeed be connected to a
5 particular intermediate level of anthropogenic disturbance, as suggested by an extended
6 interpretation of the intermediate disturbance hypothesis to a diversity of interactions between
7 vegetation and geomorphological patterns.
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12 Although our conclusions are supported statistically, the sample was not replicated for levels of
13 disturbance and time. Moreover, the range of possible anthropogenic drivers of disturbance was
14 limited to the sub-reach scale of analysis, to water resource development and one ecoregion. This
15 should be taken into account when generalizing to other rivers. Future work should therefore
16 include follow-up sampling designed to evaluate whether the observed patterns are retained in
17 different biogeographical regions, under different drivers and levels of anthropogenic disturbance
18 and also whether they continue in the long term. Finally, the role of major flood events on the
19 interaction between riparian vegetation and geomorphic patterns might also be taken into account.
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Figure captions

Fig. 1 - Location of the three studied rivers (dotted lines) with boundaries of administrative regions (continuous line) and the sub-reaches where the sampling was done (grey polygons). B: Brenta, P: Piave, T: Tagliamento.

Fig. 2 - The studied sub-reaches, frequency of landform types (fp: floodplain, ba: bar, is: island) in the plots, current width of active channel (box-whisker plots).

Fig. 3 - Box-and-whisker plot of geomorphic variables in each of three landform types (ba: bar, is: island, fp: floodplain) identified along three gravel-bed rivers (P: Piave, T: Tagliamento, B: Brenta), with increasing intensity of anthropogenic disturbance ($T < P < B$). Black dot: median. Box margins: 25th and 75th percentiles. Outliers are plotted individually. Letters represent the results of Tukey all-pair comparisons (values of islands of the Brenta river were not used in the analysis). In case they were transformed, the values are back transformed to the original ones.

Fig. 4 - Box-and-whisker plot of stand variables in each of three landform types (ba: bar, is: island, fp: floodplain) identified along three gravel-bed rivers (P: Piave, T: Tagliamento, B: Brenta), with increasing intensity of anthropogenic disturbance ($T < P < B$). Black dot: median. Box margins: 25th and 75th percentiles. Outliers are plotted individually. Letters represent the results of Tukey all-pair comparisons (values of islands of the Brenta river were not used in the analysis). In case they were transformed, the values are back transformed to the original ones.

Fig. 5 - RDA ordination biplot of the observations on 234 plots along cross transects in three gravel-bed rivers. Rivers. Arrows represent the biplot scores of environmental and stand variables (Dm: grain size, Au: geomorphic persistence, Qm: elevation above thalweg, Db: mean DBH, At: mean tree age, Sf: fine sediment, Nl: number of woody species). The centroids of combinations of river and landform types are denoted by plan figures with size proportional to increasing intensity of anthropogenic disturbance (Tagliamento $<$ Piave $<$ Brenta) and variable shapes depending on the landform type. Lower case codes are the species (bv: *Berberis vulgaris*, fx: *Fraxinus oxycarpa*, fe: *Fraxinus excelsior*, rf: *Rubus caesius*, cs: *Cornus sanguinea*, ca: *Corylus avellana*, lx: *Lonicera xylosteum*, pa: *Picea abies*, qr: *Quercus robur*, ap: *Acer pseudoplatanus*, ps: *Pinus sylvestris*, rp: *Robinia pseudoacacia*, hh: *Hedera helix*, sa: *Salix alba*, ai: *Alnus incana*, fa: *Frangula alnus*, qp: *Quercus pubescens*, vl: *Viburnum lantana*, ag: *Alnus glutinosa*, af: *Amorpha fruticosa*, oc: *Ostrya carpinifolia*, fo: *Fraxinus ornus*, lv: *Ligustrum vulgare*, pg: *Populus nigra*, se: *Salix eleagnos*).

Fig. 6 - Schematic diagram showing how the variance of species constrained by geomorphological patterns increases passing from the less anthropogenic disturbed Tagliamento River to the intermediate-disturbed Piave River and then reduces again to the lowest level in the highly

disturbed Brenta River. Schematic drawings of the three river models are modified, with permission, from [60].

Table captions

Tab. 1 - Main characteristics of the three studied rivers associated to gravel mining and dam alterations (from [62]).

Tab. 2 - Number and length of cross sections and plots surveyed in three gravel-bed rivers (Brenta, Piave, Tagliamento).

Tab. 3 - Indicator woody species ($\alpha = 0.05$, 999 perm.) of three landform types (F: floodplain, B: bar, I: island) identified along three gravel-bed rivers (Brenta, Piave, Tagliamento) with increasing intensity of human impact (Brenta > Piave > Tagliamento). In grey: the combination of landform types most strongly related to the species pattern.